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Sensitivity analysis for a structured juvenile–adult model

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A B S T R A C T

In this paper, we consider a model which describes the dynamics of an amphibian population where individuals are divided into juveniles and adults. We derive sensitivity partial differential equations for the sensitivities of the solution with respect to the reproduction and mortality rates for adults. We also present numerical results to show the application of these equations to an amphibian population of green tree frogs (*Hyla cinerea*).

1. Introduction

In this paper, we consider the following structured juvenile–adult population model:

$$\begin{aligned}
&J_t(a,t)+J_a(a,t)+\nu(a)J(a,t)=0, && (a,t)\in(0,\bar{a})\times(0,T),\\
&A_t(x,t)+(g(x)A(x,t))_x+\mu(\varphi(t))A(x,t)=0, && (x,t)\in(\underline{x},\bar{x})\times(0,T),\\
&J(0,t)=\int_{\underline{x}}^{\bar{x}}\beta(\varphi(t))A(x,t)dx, && t\in(0,T),\\
&g(\underline{x})A(\underline{x},t)=J(\bar{a},t), && t\in(0,T),\\
&J(a,0)=J_0(a), && a\in[0,\bar{a}],\\
&A(x,0)=A_0(x), && x\in[\underline{x},\bar{x}],
\end{aligned}\tag{1.1}$$

where $J(a,t)$ and $A(x,t)$ denote the density of juveniles of age a and adults of size x at time t, respectively, $\bar{a}$ denotes the age at which juveniles metamorphose into adults of minimum size $\underline{x}$, and $\bar{x}$ denotes the maximum size of adults. The function $\varphi(t)=\int_{\underline{x}}^{\bar{x}}A(x,t)dx$ is the total population of adults. The parameters ν and μ are the mortality rates for juveniles and adults, respectively. The functions g and β are the growth and reproduction rates for adults, respectively. Motivated by an amphibian population of green tree frogs (*Hyla cinerea*), we recently developed such a model in [1]. We assumed that juveniles live in an environment with abundant resources and thus do not compete, while adults live in an environment with limiting resource and thus competition between them takes place. We then established existence–uniqueness results and discussed the long-time behavior of the solution of the model via a comparison principle.

Our objective here is to conduct sensitivity analysis for model (1.1). The importance of sensitivity equations has long been recognized as they provide a measure of model response (output) to variation in the underlying model parameters (e.g., see [2,3] and the references therein). The derivation of sensitivity equations for discrete structured population models (matrix models) has received a great deal of attention in the past few decades (see [2] and the many references therein).

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However, little work has been done on the derivation of sensitivity equations for continuous structured population models which are of Mckendrick–von Foerster partial differential equations type. Such equations are useful for computing variances of estimated model parameters from observation data (e.g., see, [4–7]). Our motivation comes from paper [8], wherein sensitivity partial differential equations were derived for the following linear size-structured population model:

$$\begin{aligned} & u_t(x,t) + (g(x)u(x,t))_x + \mu(x)u(x,t) = 0, && (x,t) \in (0,\bar{x}) \times (0,T), \\ & g(0)u(0,t) = \int_0^{\bar{x}} \beta(x)u(x,t)dx, && t \in (0,T), \\ & u(x,0) = u_0(x), && x \in [0,\bar{x}]. \end{aligned} \tag{1.2}$$

There are two main differences between models (1.2) and (1.1). First, (1.2) is a single equation model, but (1.1) is a system of coupled equations. Second, the vital rates in (1.2) are linear, but the reproduction and mortality rates for adults in (1.1) are dependent on the total population of adults. Due to the different structure of model (1.1), the situation becomes more complicated, and certain techniques used for (1.2) seem not applicable to (1.1).

The paper is organized as follows. In Section 2, we establish an existence result for directional derivatives with respect to parameters. In Section 3, we derive sensitivity partial differential equations for the sensitivities of the solution with respect to the reproduction and mortality rates for adults. In Section 4, we make numerical simulations to apply these equations to the population of green tree frogs.

2. Existence of the directional derivative

To carry out our sensitivity analysis, we assume that the parameters in (1.1) satisfy the following assumptions:

(A1) $g \in C^1[\underline{x}, \bar{x}]$. Furthermore, $g(x) > 0$ for $x \in [\underline{x}, \bar{x})$ and $g(\bar{x}) = 0$.
(A2) $\nu \in L^\infty(0, \bar{a})$ is nonnegative.
(A3) $\mu \in C^1[0, \infty)$ is nonnegative with $\mu' \geq 0$.
(A4) $\beta \in C^1[0, \infty)$ is nonnegative with $\beta' \leq 0$.
(A5) $J_0 \in L^\infty(0, \bar{a})$ is nonnegative.
(A6) $A_0 \in L^\infty(\underline{x}, \bar{x})$ is nonnegative.

We first introduce the solution representation for problem (1.1) via the method of characteristics. For the first equation in (1.1), the characteristic curves can be easily obtained. For the second equation in (1.1), the characteristic curves are given by

$$\begin{cases} \dfrac{d}{ds}t(s) = 1 \\ \dfrac{d}{ds}x(s) = g(x(s)). \end{cases} \tag{2.1}$$

Under assumption (A1), Eq. (2.1) has a unique solution for any initial point $(x(s_0), t(s_0))$. Parameterizing the characteristic curves with the variable t, then a characteristic curve passing through $(\hat{x}, \hat{t})$ is given by $(X(t; \hat{x}, \hat{t}), t)$, where X satisfies

$$\frac{d}{dt}X(t; \hat{x}, \hat{t}) = g(X(t; \hat{x}, \hat{t}))$$

and $X(\hat{t}; \hat{x}, \hat{t}) = \hat{x}$. By (A1) the function X is strictly increasing, and therefore a unique inverse function $\Gamma(x; \hat{x}, \hat{t})$ exists. Let $G(x) = \Gamma(x; \underline{x}, 0)$, then $(x, G(x))$ represents the characteristic curve passing through $(\underline{x}, 0)$, and this curve divides the (x, t)-plane into two parts. Hence, the solution of (1.1) can be represented as follows:

$$J(a,t) = J_0(a-t)\exp\left(-\int_{a-t}^{a} \nu(\sigma)d\sigma\right) \quad \text{if } t \leq a, \tag{2.2}$$

$$J(a,t) = \beta(\varphi(t-a))\varphi(t-a)\exp\left(-\int_0^a \nu(\sigma)d\sigma\right) \quad \text{if } t > a, \tag{2.3}$$

$$A(x,t) = A_0(X(0;x,t))\exp\left\{-\int_0^t [g_x(X(\tau;x,t)) + \mu(\varphi(\tau))]d\tau\right\} \quad \text{if } t \leq G(x), \tag{2.4}$$

$$A(x,t) = \frac{J(\bar{a}, \Gamma(\underline{x}; x, t))}{g(\underline{x})}\exp\left\{-\int_{\Gamma(\underline{x};x,t)}^t [g_x(X(\tau;x,t)) + \mu(\varphi(\tau))]d\tau\right\} \quad \text{if } t > G(x). \tag{2.5}$$

Integrating (2.4)–(2.5) with respect to x, we obtain an integral representation for $\varphi(t)$:

$$\varphi(t) = \int_0^t J(\bar{a}, \tau)\exp\left(-\int_\tau^t \mu(\varphi(s))ds\right)d\tau + \int_{\underline{x}}^{\bar{x}} A_0(\xi)\exp\left(-\int_0^t \mu(\varphi(s))ds\right)d\xi. \tag{2.6}$$

Taking (2.2) and (2.3) into account, we further have

$$\varphi(t)=\int_0^t J_0(\bar a-\tau)c(\tau)\exp\left(-\int_\tau^t \mu(\varphi(s))ds\right)d\tau+\int_{\underline{x}}^{\bar x} A_0(\xi)\exp\left(-\int_0^t \mu(\varphi(s))ds\right)d\xi \quad \text{if } t\le \bar a, \tag{2.7}$$

$$\begin{aligned}\varphi(t) \;=\; & \int_0^{\bar a} J_0(\bar a-\tau)c(\tau)\exp\left(-\int_\tau^{\bar a} \mu(\varphi(s))ds\right)d\tau \\ & +c(\bar a)\int_{\bar a}^t \beta(\varphi(\tau-\bar a))\varphi(\tau-\bar a)\exp\left(-\int_\tau^t \mu(\varphi(s))ds\right)d\tau \\ & +\int_{\underline{x}}^{\bar x} A_0(\xi)\exp\left(-\int_0^t \mu(\varphi(s))ds\right)d\xi \quad \text{if } t>\bar a,\end{aligned} \tag{2.8}$$

where $c(\tau)=\exp\left(-\int_{\bar a-\tau}^{\bar a}\nu(\sigma)d\sigma\right)$.

As in [8], we then introduce the directional derivative of a function f with respect to a parameter θ.

Definition 2.1. Let Θ be a convex subset in some topological vector space, and $f:\mathbb{R}_+\times\Theta\to\mathbb{R}$. Given θ and $\hat\theta$ in Θ, we define the derivative $f_\theta(t;\theta,\hat\theta-\theta)$ of f at θ in the direction $\hat\theta-\theta$ to be

$$f_\theta(t;\theta,\hat\theta-\theta)=\lim_{\varepsilon\to 0^+}\frac{f(t;\theta+\varepsilon(\hat\theta-\theta))-f(t;\theta)}{\varepsilon}, \tag{2.9}$$

provided this limit exists.

We now establish an existence result which will play an important role in our sensitivity analysis.

Theorem 2.2. *For θ and $\hat\theta$ in Θ, suppose that μ and β each have a bounded directional derivative $\mu_\theta(\varphi(t);\theta,\hat\theta-\theta)$ and $\beta_\theta(\varphi(t);\theta,\hat\theta-\theta)$ on $[0,T]$, respectively, in the direction $\hat\theta-\theta$. Furthermore, we assume that μ_φ and β_φ are continuously dependent on θ. Then the directional derivative $\varphi_\theta(t;\theta,\hat\theta-\theta)$ of φ with respect to θ in the direction $\hat\theta-\theta$ exists and satisfies the following equation*

$$\begin{aligned}\psi(t) \;=\; & -\int_0^t J_0(\bar a-\tau)c(\tau)\exp\left(-\int_\tau^t \mu(\varphi(s);\theta)ds\right)\int_\tau^t \mu_\varphi(\varphi(s);\theta)\psi(s)dsd\tau \\ & -\int_{\underline{x}}^{\bar x} A_0(\xi)\exp\left(-\int_0^t \mu(\varphi(s);\theta)ds\right)d\xi\int_0^t \mu_\varphi(\varphi(s);\theta)\psi(s)ds \\ & -\int_0^t J_0(\bar a-\tau)c(\tau)\exp\left(-\int_\tau^t \mu(\varphi(s);\theta)ds\right)\int_\tau^t \mu_\theta(\varphi(s);\theta)dsd\tau \\ & -\int_{\underline{x}}^{\bar x} A_0(\xi)\exp\left(-\int_0^t \mu(\varphi(s);\theta)ds\right)d\xi\int_0^t \mu_\theta(\varphi(s);\theta)ds \quad \textit{if } t\le\bar a,\end{aligned} \tag{2.10}$$

$$\begin{aligned}\psi(t) \;=\; & -\int_0^{\bar a} J_0(\bar a-\tau)c(\tau)\exp\left(-\int_\tau^{\bar a} \mu(\varphi(s);\theta)ds\right)\int_\tau^{\bar a} \mu_\varphi(\varphi(s);\theta)\psi(s)dsd\tau \\ & +c(\bar a)\int_{\bar a}^t \beta_\varphi(\varphi(\tau-\bar a);\theta)\varphi(\tau-\bar a)\psi(t-\bar a)\exp\left(-\int_\tau^t \mu(\varphi(s);\theta)ds\right)d\tau \\ & +c(\bar a)\int_{\bar a}^t \beta(\varphi(t-\bar a);\theta)\psi(t-\bar a)\exp\left(-\int_\tau^t \mu(\varphi(s);\theta)ds\right)d\tau \\ & -c(\bar a)\int_{\bar a}^t \beta(\varphi(\tau-\bar a);\theta)\varphi(\tau-\bar a)\exp\left(-\int_\tau^t \mu(\varphi(s);\theta)ds\right)\int_\tau^t \mu_\varphi(\varphi(s);\theta)\psi(s)dsd\tau \\ & -\int_{\underline{x}}^{\bar x} A_0(\xi)\exp\left(-\int_0^t \mu(\varphi(s);\theta)ds\right)d\xi\int_0^t \mu_\varphi(\varphi(s);\theta)\psi(s)ds \\ & -c(\bar a)\int_{\bar a}^t \beta(\varphi(\tau-\bar a);\theta)\varphi(\tau-\bar a)\exp\left(-\int_\tau^t \mu(\varphi(s);\theta)ds\right)\int_\tau^t \mu_\theta(\varphi(s);\theta)dsd\tau \\ & -\int_{\underline{x}}^{\bar x} A_0(\xi)\exp\left(-\int_0^t \mu(\varphi(s);\theta)ds\right)d\xi\int_0^t \mu_\theta(\varphi(s);\theta)ds \quad \textit{if } t>\bar a,\end{aligned} \tag{2.11}$$

where $\varphi(t)=\varphi(t;\theta)$ and $\psi(t)=\varphi_\theta(t;\theta,\hat\theta-\theta)$.

Proof. We first show that there exists a unique bounded solution $\psi(t)$ of (2.10)–(2.11). Recalling Lemma 5.3 in [1], one can find a positive constant $\bar{\varphi}$ such that $\varphi(t)$ given by (2.7)–(2.8) is bounded by $\bar{\varphi}$ on $[0,\infty)$. Therefore, by assumptions (A3)–(A4), the vital rates μ,β and their derivatives are uniformly bounded. Thus, for $0\le t\le T$ with $T\le\bar{a}$, since Eq. (2.10) is a linear equation of ψ, it has a unique solution. On the other hand, for $0\le t\le T$ with $T>\bar{a}$, Eq. (2.11) is a linear equation with delay, proceeding as in [9], one can see that (2.11) has a unique solution. The boundedness of ψ follows from the application of Gronwall's inequality.

We then claim that $\varphi(t;\theta)$ is continuously dependent on θ. To prove this claim for $t\in[0,T]$ with $T\le\bar{a}$, let $C(t;\theta,\hat{\theta}-\theta)=\varphi(t;\theta+\varepsilon(\hat{\theta}-\theta))-\varphi(t;\theta)$. By (2.7), there exists a positive constant C_1 such that

$$\begin{aligned}\frac{1}{C_1}|C(t;\theta,\hat{\theta}-\theta)| \le{}& \int_0^t\int_\tau^t |\mu_\varphi(\hat{\varphi}(s);\theta+\varepsilon(\hat{\theta}-\theta))|\,|C(s;\theta,\hat{\theta}-\theta)|dsd\tau\\ &+\int_0^t\int_\tau^t \left|\mu(\varphi(s;\theta);\theta+\varepsilon(\hat{\theta}-\theta))-\mu(\varphi(s;\theta);\theta)\right|dsd\tau\\ &+\int_0^t |\mu_\varphi(\tilde{\varphi}(s);\theta+\varepsilon(\hat{\theta}-\theta))|\,|C(s;\theta,\hat{\theta}-\theta)|ds\\ &+\int_0^t \left|\mu(\varphi(s;\theta);\theta+\varepsilon(\hat{\theta}-\theta))-\mu(\varphi(s;\theta);\theta)\right|ds, \end{aligned}\tag{2.12}$$

where $\hat{\varphi}(s),\tilde{\varphi}(s)$ are between $\varphi(s;\theta)$ and $\varphi(s;\theta+\varepsilon(\hat{\theta}-\theta))$. Because $\mu_\theta(\varphi(t);\theta,\hat{\theta}-\theta)$ is bounded on $[0,T]$, $\lim_{\varepsilon\to0^+}\mu(\varphi(s;\theta);\theta+\varepsilon(\hat{\theta}-\theta))=\mu(\varphi(s;\theta);\theta)$, and thus the second term and the fourth term on the right hand side of (2.12) approach zero as $\varepsilon\to0$. Hence, by Gronwall's inequality we have that $\lim_{\varepsilon\to0^+}|C(t;\theta,\hat{\theta}-\theta)|=0$. On the other hand, making use of (2.8) and proceeding analogously, we can prove the claim for $t\in[0,T]$ with $T>\bar{a}$.

We now show that $\varphi_\theta(t;\theta,\hat{\theta}-\theta)$ exists and satisfies equations (2.10)–(2.11). For $t\in[0,T]$ with $T\le\bar{a}$, let $D(t;\theta,\hat{\theta}-\theta)=\frac{\varphi(t;\theta+\varepsilon(\hat{\theta}-\theta))-\varphi(t;\theta)}{\varepsilon}-\psi(t)$. In view of (2.7) and (2.10), we find that there exists a positive constant C_2 such that

$$\begin{aligned}\frac{1}{C_2}|D(t;\theta,\hat{\theta}-\theta)| \le{}& \int_0^t\int_\tau^t |\mu_\varphi(\hat{\varphi}(s);\theta+\varepsilon(\hat{\theta}-\theta))|\,|D(s;\theta,\hat{\theta}-\theta)|dsd\tau\\ &+\int_0^t\left|\exp\left(-\int_\tau^t\hat{\mu}(s)ds\right)\int_\tau^t\mu_\varphi(\hat{\varphi}(s);\theta+\varepsilon(\hat{\theta}-\theta))\psi(s)ds\right.\\ &\left.-\exp\left(-\int_\tau^t\mu(\varphi(s;\theta);\theta)ds\right)\int_\tau^t\mu_\varphi(\varphi(s;\theta);\theta)\psi(s)ds\right|d\tau\\ &+\int_0^t\int_\tau^t\left|\frac{\mu(\varphi(s;\theta);\theta+\varepsilon(\hat{\theta}-\theta))-\mu(\varphi(s;\theta);\theta)}{\varepsilon}-\mu_\theta(\varphi(s;\theta);\theta)\right|dsd\tau\\ &+\int_0^t\left|\exp\left(-\int_\tau^t\hat{\mu}(s)ds\right)\int_\tau^t\mu_\theta(\varphi(s;\theta);\theta)ds\right.\\ &\left.-\exp\left(-\int_\tau^t\mu(\varphi(s;\theta);\theta)ds\right)ds\int_\tau^t\mu_\theta(\varphi(s;\theta);\theta)ds\right|d\tau\\ &+\int_0^t|\mu_\varphi(\tilde{\varphi}(s);\theta+\varepsilon(\hat{\theta}-\theta))|\,|D(s;\theta,\hat{\theta}-\theta)|ds\\ &+\left|\exp\left(-\int_0^t\tilde{\mu}(s)ds\right)\int_\tau^t\mu_\varphi(\tilde{\varphi}(s);\theta+\varepsilon(\hat{\theta}-\theta))\psi(s)ds\right.\\ &\left.-\exp\left(-\int_0^t\mu(\varphi(s;\theta);\theta)ds\right)\int_0^t\mu_\varphi(\varphi(s;\theta);\theta)\psi(s)ds\right|\\ &+\int_0^t\left|\frac{\mu(\varphi(s;\theta);\theta+\varepsilon(\hat{\theta}-\theta))-\mu(\varphi(s;\theta);\theta)}{\varepsilon}-\mu_\theta(\varphi(s;\theta);\theta)\right|ds\\ &+\left|\exp\left(-\int_0^t\tilde{\mu}(s)ds\right)\int_0^t\mu_\theta(\varphi(s;\theta);\theta)ds\right.\\ &\left.-\exp\left(-\int_0^t\mu(\varphi(s;\theta);\theta)ds\right)ds\int_0^t\mu_\theta(\varphi(s;\theta);\theta)ds\right|, \end{aligned}\tag{2.13}$$

where $\hat{\mu}(s)$, $\tilde{\mu}(s)$ are between $\mu(\varphi(s;\theta);\theta)$ and $\mu(\varphi(s;\theta+\varepsilon(\hat{\theta}-\theta));\theta+\varepsilon(\hat{\theta}-\theta))$, and $\hat{\varphi}(s)$, $\tilde{\varphi}(s)$ are between $\varphi(s;\theta)$ and $\varphi(s;\theta+\varepsilon(\hat{\theta}-\theta))$. Because both φ and μ_φ are continuously dependent on θ, the second term, the fourth term, the sixth term, and the eighth term on the right hand side of (2.13) approach zero as $\varepsilon \to 0$. Moreover, because μ has a bounded directional derivative $\mu_\theta(\varphi(t);\theta,\hat{\theta}-\theta)$ on $[0,T]$ in the direction $\hat{\theta}-\theta$, the third term and the seventh term on the right hand side of (2.13) converge to zero as $\varepsilon \to 0$. Hence, the application of Gronwall's inequality yields $\lim_{\varepsilon\to 0^+}|D(t;\theta,\hat{\theta}-\theta)| = 0$. On the other hand, by virtue of (2.8) and (2.11), the same existence result can be established in a similar manner for $t \in [0,T]$ with $T > \bar{a}$. □

3. Sensitivity equations

In this section, we derive sensitivity partial differential equations for the sensitivities of the solution (J,A) with respect to the reproduction rate β and the mortality rate μ. For simplicity, we use $h(\theta)$ to denote a given direction in the respective parameter space. We first consider the sensitivity of (J,A) with respect to β. By the solution representation formula (2.2)–(2.5) and the definition of the directional derivative (2.9), we have that

$$J_\beta(a,t;\beta,h) = 0 \quad \text{if } t \le a, \tag{3.1}$$

$$\begin{aligned} J_\beta(a,t;\beta,h) \;=\; &\big\{[\beta_\varphi(\varphi(t-a;\beta,h);\beta,h)\varphi_\beta(t-a;\beta,h)+h(\beta)]\varphi(t-a;\beta,h)\\ &+\beta(\varphi(t-a;\beta,h);\beta,h)\varphi_\beta(t-a;\beta,h)\big\}\exp\left(-\int_0^a \nu(\sigma)d\sigma\right) \quad \text{if } t > a, \end{aligned} \tag{3.2}$$

$$A_\beta(x,t;\beta,h) = -A(x,t;\beta,h)\int_0^t \mu_\varphi(\varphi(\tau;\beta,h);\beta,h)\varphi_\beta(\tau;\beta,h)d\tau \quad \text{if } t \le G(x), \tag{3.3}$$

$$\begin{aligned} A_\beta(x,t;\beta,h) \;=\; &\frac{J_\beta(\bar{a},\Gamma(\underline{x};x,t);\beta,h)}{g(\underline{x})}\exp\left\{-\int_{\Gamma(\underline{x};x,t)}^t [g_x(X(\tau;x,t))+\mu(\varphi(\tau;\beta,h);\beta,h)]d\tau\right\}\\ &-A(x,t;\beta,h)\int_{\Gamma(\underline{x};x,t)}^t \mu_\varphi(\varphi(\tau;\beta,h);\beta,h)\varphi_\beta(\tau;\beta,h)d\tau \quad \text{if } t > G(x). \end{aligned} \tag{3.4}$$

We now introduce the following system:

$$\begin{aligned} &K_t(a,t)+K_a(a,t)+\nu(a)K(a,t)=0, && (a,t)\in(0,\bar{a})\times(0,T),\\ &B_t(x,t)+(g(x)B(x,t))_x+\mu(\varphi(t))B(x,t) = -\mu_\varphi(\varphi(t))\varphi_\beta(t)A(x,t), && (x,t)\in(\underline{x},\bar{x})\times(0,T),\\ &K(0,t)=[\beta_\varphi(\varphi(t))\varphi_\beta(t)+h(\beta)]\varphi(t)+\beta(\varphi(t))\varphi_\beta(t), && t\in(0,T),\\ &g(\underline{x})B(\underline{x},t)=K(\bar{a},t), && t\in(0,T),\\ &K(a,0)=0, && a\in[0,\bar{a}],\\ &B(x,0)=0, && x\in[\underline{x},\bar{x}]. \end{aligned} \tag{3.5}$$

Since the above equations are linear, it can be easily shown that there exists a unique solution (K,B) of (3.5). Via the method of characteristics, we find that

$$K(a,t) = 0 \quad \text{if } t \le a, \tag{3.6}$$

$$\begin{aligned} K(a,t) \;=\; &\big\{[\beta_\varphi(\varphi(t-a))\varphi_\beta(t-a)+h(\beta)]\varphi(t-a)\\ &+\beta(\varphi(t-a))\varphi_\beta(t-a)\big\}\exp\left(-\int_0^a \nu(\sigma)d\sigma\right) \quad \text{if } t > a. \end{aligned} \tag{3.7}$$

Furthermore, in view of (2.4), we have that

$$\begin{aligned} B(x,t) &= -\int_0^t \exp\left\{-\int_\tau^t [g_x(X(s;x,t))+\mu(\varphi(s))]ds\right\}\mu_\varphi(\varphi(\tau))\varphi_\beta(\tau)A(X(\tau;x,t),\tau)d\tau\\ &= -A_0(X(0;x,t))\exp\left\{-\int_0^t [g_x(X(s;x,t))+\mu(\varphi(s))]ds\right\}\int_0^t \mu_\varphi(\varphi(\tau))\varphi_\beta(\tau)d\tau\\ &= -A(x,t)\int_0^t \mu_\varphi(\varphi(\tau))\varphi_\beta(\tau)d\tau \quad \text{if } t \le G(x), \end{aligned} \tag{3.8}$$

and by virtue of (2.5), we have that

$$\begin{aligned} B(x,t) &= \frac{K(\bar{a},\Gamma(\underline{x};x,t))}{g(\underline{x})}\exp\left\{-\int_{\Gamma(\underline{x};x,t)}^{t}[g_x(X(\tau;x,t))+\mu(\varphi(\tau))]d\tau\right\} \\ &\quad -\int_{\Gamma(\underline{x};x,t)}^{t}\exp\left\{-\int_{\tau}^{t}[g_x(X(s;x,t))+\mu(\varphi(s))]ds\right\}\mu_\varphi(\varphi(\tau))\varphi_\beta(\tau)A(X(\tau;x,t),\tau)d\tau \\ &= \frac{K(\bar{a},\Gamma(\underline{x};x,t))}{g(\underline{x})}\exp\left\{-\int_{\Gamma(\underline{x};x,t)}^{t}[g_x(X(\tau;x,t))+\mu(\varphi(\tau))]d\tau\right\} \\ &\quad -\frac{J(\bar{a},\Gamma(\underline{x};x,t))}{g(\underline{x})}\exp\left\{-\int_{\Gamma(\underline{x};x,t)}^{t}[g_x(X(\tau;x,t))+\mu(\varphi(\tau))]d\tau\right\} \\ &\quad \cdot\int_{\Gamma(\underline{x};x,t)}^{t}\mu_\varphi(\varphi(\tau))\varphi_\beta(\tau)d\tau \\ &= \frac{K(\bar{a},\Gamma(\underline{x};x,t))}{g(\underline{x})}\exp\left\{-\int_{\Gamma(\underline{x};x,t)}^{t}[g_x(X(\tau;x,t))+\mu(\varphi(\tau))]d\tau\right\} \\ &\quad -A(x,t)\int_{\Gamma(\underline{x};x,t)}^{t}\mu_\varphi(\varphi(\tau))\varphi_\beta(\tau)d\tau \quad \text{if } t>G(x). \end{aligned} \tag{3.9}$$

Comparing (3.6)–(3.9) with (3.1)–(3.4), we find that $J_\beta = K$ and $A_\beta = B$, and thus system (3.5) can be used to solve for the sensitivity of (J, A) with respect to β.

We then consider the sensitivity of (J, A) with respect to μ. By the solution representation formula (2.2)–(2.5), we have that

$$J_\mu(a,t;\mu,h) = 0 \quad \text{if } t\le a, \tag{3.10}$$

$$\begin{aligned} J_\mu(a,t;\mu,h) &= [\beta_\varphi(\varphi(t-a;\mu,h);\mu,h)\varphi(t-a;\mu,h) \\ &\quad +\beta(\varphi(t-a;\mu,h);\mu,h)]\varphi_\mu(t-a;\mu,h)\exp\left(-\int_0^a\nu(\sigma)d\sigma\right) \quad \text{if } t>a, \end{aligned} \tag{3.11}$$

$$A_\mu(x,t;\mu,h) = -A(x,t;\mu,h)\int_0^t[\mu_\varphi(\varphi(\tau;\mu,h);\mu,h)\varphi_\mu(\tau;\mu,h)+h(\mu)]d\tau \quad \text{if } t\le G(x), \tag{3.12}$$

$$\begin{aligned} A_\mu(x,t;\mu,h) &= \frac{J_\mu(\bar{a},\Gamma(\underline{x};x,t);\mu,h)}{g(\underline{x})}\exp\left\{-\int_{\Gamma(\underline{x};x,t)}^{t}[g_x(X(\tau;x,t))+\mu(\varphi(\tau;\mu,h);\mu,h)]d\tau\right\} \\ &\quad -A(x,t;\mu,h)\int_{\Gamma(\underline{x};x,t)}^{t}[\mu_\varphi(\varphi(\tau;\mu,h);\mu,h)\varphi_\mu(\tau;\mu,h)+h(\mu)]d\tau \quad \text{if } t>G(x). \end{aligned} \tag{3.13}$$

We now introduce the following system:

$$\begin{array}{ll} L_t(a,t)+L_a(a,t)+\nu(a)L(a,t)=0, & (a,t)\in(0,\bar{a})\times(0,T), \\ C_t(x,t)+(g(x)C(x,t))_x+\mu(\varphi(t))C(x,t)=-[\mu_\varphi(\varphi(t))\varphi_\mu(t)+h(\mu)]A(x,t), & (x,t)\in(\underline{x},\bar{x})\times(0,T), \\ L(0,t)=[\beta_\varphi(\varphi(t))\varphi(t)+\beta(\varphi(t))]\varphi_\mu(t), & t\in(0,T), \\ g(\underline{x})C(\underline{x},t)=L(\bar{a},t), & t\in(0,T), \\ L(a,0)=0, & a\in[0,\bar{a}], \\ C(x,0)=0, & x\in[\underline{x},\bar{x}]. \end{array} \tag{3.14}$$

Again we can see that there exists a unique solution (L, C) of (3.14). Using the method of characteristics, we find that

$$L(a,t) = 0 \quad \text{if } t\le a, \tag{3.15}$$

$$L(a,t) = [\beta_\varphi(\varphi(t-a))\varphi(t-a)+\beta(\varphi(t-a))]\varphi_\mu(t-a)\exp\left(-\int_0^a\nu(\sigma)d\sigma\right) \quad \text{if } t>a. \tag{3.16}$$

Moreover, as in (3.8) we have that

$$\begin{aligned} C(x,t) &= -\int_0^t\exp\left\{-\int_\tau^t[g_x(X(s;x,t))+\mu(\varphi(s))]ds\right\}\cdot[\mu_\varphi(\varphi(\tau))\varphi_\mu(\tau)+h(\mu)]A(X(\tau;x,t),\tau)d\tau \\ &= -A(x,t)\int_0^t[\mu_\varphi(\varphi(\tau))\varphi_\mu(\tau)+h(\mu)]d\tau \quad \text{if } t\le G(x), \end{aligned} \tag{3.17}$$

and as in (3.9) we have that

$$\begin{aligned} C(x,t) &= \frac{L(\bar{a},\Gamma(\underline{x};x,t))}{g(\underline{x})}\exp\left\{-\int_{\Gamma(\underline{x};x,t)}^{t}[g_x(X(\tau;x,t))+\mu(\varphi(\tau))]d\tau\right\} \\ &\quad -\int_{\Gamma(\underline{x};x,t)}^{t}\exp\left\{-\int_{\tau}^{t}[g_x(X(s;x,t))+\mu(\varphi(s))]ds\right\} \\ &\quad \cdot[\mu_\varphi(\varphi(\tau))\varphi_\beta(\tau)+h(\mu)]A(X(\tau;x,t),\tau)d\tau \\ &= \frac{L(\bar{a},\Gamma(\underline{x};x,t))}{g(\underline{x})}\exp\left\{-\int_{\Gamma(\underline{x};x,t)}^{t}[g_x(X(\tau;x,t))+\mu(\varphi(\tau))]d\tau\right\} \\ &\quad -A(x,t)\int_{\Gamma(\underline{x};x,t)}^{t}[\mu_\varphi(\varphi(\tau))\varphi_\mu(\tau)+h(\mu)]d\tau \quad \text{if } t>G(x). \end{aligned} \tag{3.18}$$

Comparing (3.15)–(3.18) with (3.10)–(3.13) yields that $J_\mu = L$ and $A_\mu = C$, and hence system (3.14) can be used to solve for the sensitivity of (J, A) with respect to μ.

Remark 3.1. With the equivalence $J_\beta = K, A_\beta = B$ and $J_\mu = L, A_\mu = C$, one can see that $\varphi_\beta(t)$ and $\varphi_\mu(t)$ can be replaced with $\int_{\underline{x}}^{\bar{x}} B(x,t)dx$ and $\int_{\underline{x}}^{\bar{x}} C(x,t)dx$ in (3.5) and (3.14), respectively.

Remark 3.2. All the results hold for $\mu = \mu(t,\varphi)$ and $\beta = \beta(t,\varphi)$ under the assumptions that $\mu, \beta \in C([0,\infty)\times[0,\bar{\varphi}])$ are continuously differentiable with respect to φ.

4. Numerical results for a green tree frog population

The focus of this section is to apply the theory developed earlier to study the sensitivity of a green tree frog population to reproduction and mortality rates. In order to make numerical simulations, we first need a method for solving the structured juvenile–adult model (1.1). To this end, we utilize the finite-difference approximation scheme detailed below which we developed in [10]. We divide the intervals $[0,\bar{a}]$, $[\underline{x},\bar{x}]$ and $[0,T]$ into m, n and l subintervals, respectively. The following notation will be used throughout this section: $\Delta a = \bar{a}/m$, $\Delta x = (\bar{x}-\underline{x})/n$ and $\Delta t = T/l$ denote the age, size, and time mesh lengths, respectively. The mesh points are given by $a_i = i\Delta a, i = 0,1,\ldots,m$, $x_j = \underline{x}+j\Delta x, j = 0,1,\ldots,n$, $t_k = k\Delta t, k = 0,1,\ldots,l$. We denote by J_i^k, A_j^k, and φ^k the finite difference approximation of $J(a_i,t_k), A(x_j,t_k)$, and $\varphi(t_k)$, respectively, and let

$$\nu_i = \nu(a_i), \qquad g_j = g(x_j), \qquad \mu^k = \mu(t^k,\varphi^k), \qquad \beta^k = \beta(t^k,\varphi^k).$$

We then discretize system (1.1) using the following explicit finite difference approximation

$$\begin{aligned} &\frac{J_i^{k+1}-J_i^k}{\Delta t}+\frac{J_i^k-J_{i-1}^k}{\Delta a}+\nu_i^kJ_i^k = 0, && 0\le k\le l-1,\ 1\le i\le m, \\ &\frac{A_j^{k+1}-A_j^k}{\Delta t}+\frac{g_j^kA_j^k-g_{j-1}^kA_{j-1}^k}{\Delta x}+\mu_j^kA_j^k = 0, && 0\le k\le l-1,\ 1\le j\le n, \\ &J_0^{k+1} = \sum_{j=1}^{n}\beta_j^{k+1}A_j^{k+1}\Delta x, \qquad g_0^{k+1}A_0^{k+1} = J_m^{k+1}, && 0\le k\le l-1, \\ &\varphi^{k+1} = \sum_{j=1}^{n}A_j^{k+1}\Delta x, && 0\le k\le l-1 \end{aligned} \tag{4.1}$$

with the initial conditions

$$J_0^0 = J_0(0), \qquad J_i^0 = \frac{1}{\Delta a}\int_{(i-1)\Delta a}^{i\Delta a}J_0(a)da, \quad i = 1,2,\ldots,m,$$

$$A_0^0 = A_0(0), \qquad A_j^0 = \frac{1}{\Delta x}\int_{(j-1)\Delta x}^{j\Delta x}A_0(x)dx, \quad j = 1,2,\ldots,n.$$

The following condition concerning Δt, Δa and Δx is imposed throughout this section.

(A7) Assume that Δt, Δa and Δx are chosen such that

$$\Delta t\left(\frac{1}{\Delta a}+\omega\right)\le 1 \quad \text{and} \quad \omega\Delta t\left(\frac{1}{\Delta x}+1\right)\le 1,$$

where ω is a positive constant for which $\sup_{[0,\infty)\times[0,\bar{\varphi}]}\mu(t,\varphi)\le\omega$ and $\sup_{[0,\infty)\times[0,\bar{\varphi}]}\beta(t,\varphi)\le\omega$. Equivalently, we can write (4.1) as the following system of linear equations:

$$\begin{aligned}
&J_i^{k+1}=\frac{\Delta t}{\Delta a}J_{i-1}^k+\left(1-\frac{\Delta t}{\Delta a}-\Delta t\nu_i^k\right)J_i^k, && 0\le k\le l-1,\ 1\le i\le m,\\
&A_j^{k+1}=\frac{\Delta t}{\Delta x}g_{j-1}^kA_{j-1}^k+\left(1-\frac{\Delta t}{\Delta x}g_j^k-\Delta t\mu_j^k\right)A_j^k, && 0\le k\le l-1,\ 1\le j\le n,\\
&J_0^{k+1}=\sum_{j=1}^n\beta_j^{k+1}A_j^{k+1}\Delta x,\qquad g_0^{k+1}A_0^{k+1}=J_m^{k+1}, && 0\le k\le l-1,\\
&\varphi^{k+1}=\sum_{j=1}^nA_j^{k+1}\Delta x, && 0\le k\le l-1.
\end{aligned}\tag{4.2}$$

Under the assumptions (A1)–(A7), it is shown in [10] that system (4.2) has a unique solution satisfying $[J_0^{k+1},J_1^{k+1},\dots,J_m^{k+1},A_0^{k+1},A_1^{k+1},\dots,A_n^{k+1}]\ge\overrightarrow{\mathbf{0}}$, $k=0,1,\dots,l-1$, and this solution converges to the solution (J,A) of (1.1).

We now conduct the sensitivity analysis for a green tree frog population model. For this purpose, we choose the vital rates as follows (cf. [5,11,12]):

$$\nu=\alpha_7,\qquad \mu=\sum_{i=0}^3\alpha_{i+2}c_i(t)(1+\alpha_6\varphi),\quad\text{and}\quad g=\alpha_1(6-x),\tag{4.3}$$

where all α_i $(1\le i\le 7)$ are positive constants, and $c_i(t)$ $(0\le i\le 3)$ are given by

$$c_0(t)=\begin{cases}1-t/2, & 0\le t\le 2\\ 0, & \text{otherwise}\end{cases}$$

$$c_1(t)=\begin{cases}t/2, & 0\le t\le 2\\ 2-t/2, & 2\le t\le 4\\ 0, & \text{otherwise}\end{cases}$$

$$c_2(t)=\begin{cases}t/2-1, & 2\le t\le 4\\ 3-t/2, & 4\le t\le 6\\ 0, & \text{otherwise}\end{cases}$$

$$c_3(t)=\begin{cases}t/2-2, & 4\le t\le 6\\ 0, & \text{otherwise.}\end{cases}$$

On the time interval [0, 1], the function β is defined as

$$\beta(t)=\begin{cases}0 & t\in[0,0.3-\epsilon]\cup[0.6,1]\\ 90/(0.3-\epsilon) & t\in[0.3,0.6-\epsilon]\\ 90(t+\epsilon-0.3)/\epsilon(0.3-\epsilon) & t\in(0.3-\epsilon,0.3)\\ 90(0.6-t)/\epsilon(0.3-\epsilon) & t\in(0.6-\epsilon,0.6),\end{cases}$$

where ϵ is a sufficiently small positive constant. Then, β is extended periodically over any time interval $[t,t+1]$, $t=1,2,\dots$ in a similar manner.

We first consider the numerical computation of the sensitivity of (J,A) with respect to β. Since β is a function of t only, we let the direction $h=1$ when we take the directional derivative of (J,A) with respect to β. Noticing Remark 3.1, we discretize system (3.5) to obtain the following system of linear equations:

$$\begin{aligned}
&K_i^{k+1}=\frac{\Delta t}{\Delta a}K_{i-1}^k+\left(1-\frac{\Delta t}{\Delta a}-\Delta t\nu_i\right)K_i^k, && 0\le k\le l-1,\ 1\le i\le m,\\
&B_j^{k+1}=\frac{\Delta t}{\Delta x}g_{j-1}B_{j-1}^k+\left(1-\frac{\Delta t}{\Delta x}g_j-\Delta t\mu^k\right)B_j^k-\Delta t\mu_\varphi^k\psi^kA_j^k, && 0\le k\le l-1,\ 1\le j\le n,\\
&K_0^{k+1}=\sum_{j=1}^n(\beta^{k+1}B_j^{k+1}+A_j^{k+1})\Delta x,\qquad g_0B_0^{k+1}=K_m^{k+1}, && 0\le k\le l-1,\\
&\varphi^{k+1}=\sum_{j=1}^nA_j^{k+1}\Delta x,\qquad \psi^{k+1}=\sum_{j=1}^nB_j^{k+1}\Delta x, && 0\le k\le l-1
\end{aligned}\tag{4.4}$$

with the initial conditions

$$K_i^0=0,\quad i=0,1,\dots,m,\qquad B_j^0=0,\quad j=0,1,\dots,n.$$

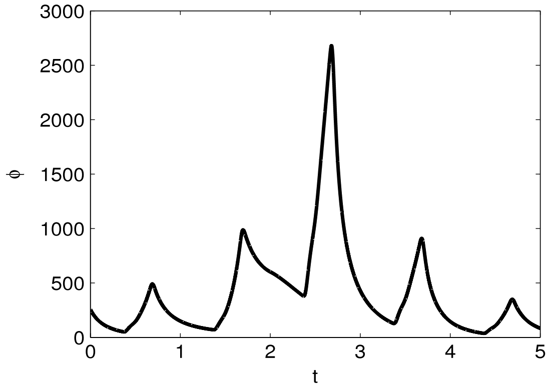

Fig. 1. Adult population in 5 year period.

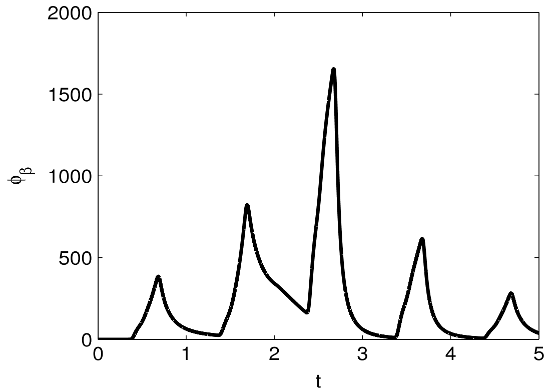

Fig. 2. Sensitivity of adult population φ with respect to β in 5 year period.

We then consider the numerical computation of the sensitivity of (J, A) with respect to μ. Since μ of (4.3) is linear in φ, we choose the direction $h = 15\alpha_6\varphi$ when we take the directional derivative of (J, A) with respect to μ. We discretize system (3.14) to obtain the following system of linear equations:

$$
\begin{aligned}
L_i^{k+1} &= \frac{\Delta t}{\Delta a} L_{i-1}^k + \left(1 - \frac{\Delta t}{\Delta a} - \Delta t \nu_i\right) L_i^k, && 0 \le k \le l-1,\ 1 \le i \le m,\\
C_j^{k+1} &= \frac{\Delta t}{\Delta x} g_{j-1} C_{j-1}^k + \left(1 - \frac{\Delta t}{\Delta x} g_j - \Delta t \mu^k\right) C_j^k - \Delta t(\mu_\varphi^k \psi^k + 15\alpha_6\varphi^k) A_j^k, && 0 \le k \le l-1,\ 1 \le j \le n,\\
L_0^{k+1} &= \sum_{j=1}^n \beta^{k+1} C_j^{k+1} \Delta x, \qquad g_0 C_0^{k+1} = L_m^{k+1}, && 0 \le k \le l-1,\\
\varphi^{k+1} &= \sum_{j=1}^n A_j^{k+1} \Delta x, \qquad \psi^{k+1} = \sum_{j=1}^n C_j^{k+1} \Delta x, && 0 \le k \le l-1
\end{aligned}
\tag{4.5}
$$

with the initial conditions

$$L_i^0 = 0, \quad i = 0, 1, \ldots, m, \qquad C_j^0 = 0, \quad j = 0, 1, \ldots, n.$$

As a demonstration of the following values, which were obtained by fitting the model to field data in [11], are chosen to numerically simulate the sensitivity equations: $\alpha_1 = 0.489$, $\alpha_2 = 3.400$, $\alpha_3 = 0.232$, $\alpha_4 = 2.908$, $\alpha_5 = 3.093$, $\alpha_6 = 0.00343$, and $\alpha_7 = 28.185$. Also we choose $\bar{a} = 5/52$, $\underline{x} = 1.5$, $\overline{x} = 6$, $\Delta a = 1/416$, $\Delta x = 1/400$, $\Delta t = 1/4160$, $J(a, 0) = 0$, $A(x, 0) = 615.96 \exp(-0.75x)$.

In Fig. 1, we plot the numerical solution for the adult population φ over a period of 5 years. Note that the population fluctuates from year to year due to the time-dependent mortality and reproduction rates of adults. Furthermore, the adult population level is significantly higher during the third year and lowest during year 5. This agrees with statistical estimates obtained from field observations using a capture–mark–recapture experiment [11]. In Figs. 2 and 3, we plot the numerical

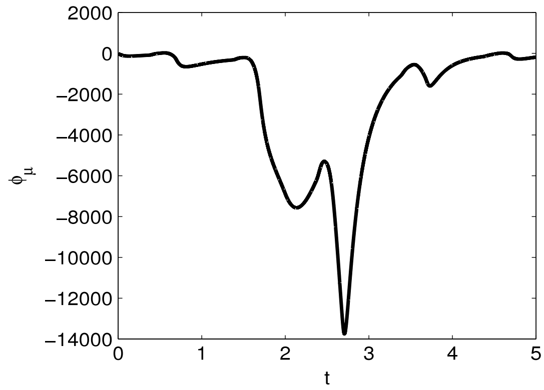

Fig. 3. Sensitivity of adult population φ with respect to μ in 5 year period.

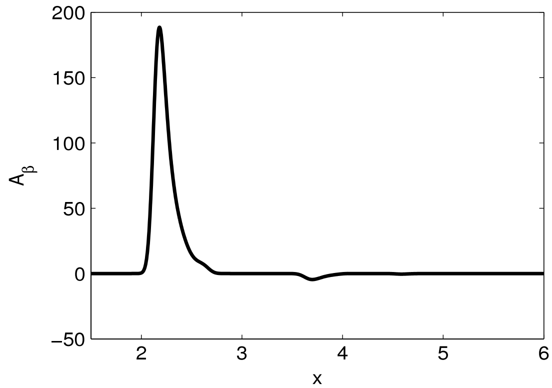

Fig. 4. Sensitivity of population density A with respect to β at $t = 5$.

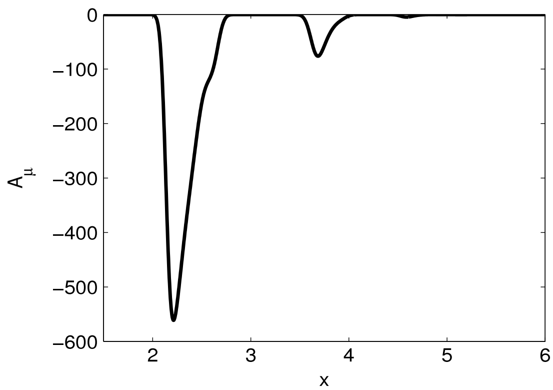

Fig. 5. Sensitivity of population density A with respect to μ at $t = 5$.

solution for the sensitivity of the total population with respect to β and μ, respectively. The numerical solution of the sensitivities of the adult population density with respect to β and μ are plotted in Figs. 4 and 5, respectively. Clearly, the results indicate that for these parameter values the total population of adults is much more sensitive to mortality than to reproduction. Furthermore, they show that during the time interval $t \in [2.5, 3]$ years the sensitivity to mortality and reproduction reaches it highest magnitude for the five year simulation. Note that this is the time interval during which the adult population reaches its highest levels (see Fig. 1).

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